

WINTER FORAGING OF LONG-TAILED DUCKS (*CLANGULA HYEMALIS*) EXPLOITING DIFFERENT BENTHIC COMMUNITIES IN THE BALTIC SEA

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ABSTRACT.—We studied the feeding ecology of Long-tailed Ducks (*Clangula hyemalis*) in two different marine benthic habitats in the Baltic Sea to determine whether there were differences in diet choice, foraging selectivity, body condition, and bird abundance. Our results corroborate earlier suggestions that Long-tailed Ducks exhibit ecological plasticity in selecting winter habitat and food. The majority of Long-tailed Ducks occurred in hard-bottom habitats where they relied on the bivalve *Mytilus edulis*; however, some of the population wintered in less productive, soft-bottom habitats where they employed a prey-selective foraging strategy, in which they fed on less abundant, but energy rich, crustaceans. Both strategies were apparently viable, as dissected birds in both habitats were in good body condition and had substantial fat reserves. Received 20 April 2004, accepted 11 February 2005.

The Long-tailed Duck (*Clangula hyemalis*) is the most abundant sea duck wintering in the Baltic Sea, where estimated numbers exceed 4 million. Wintering Long-tailed Ducks inhabit a variety of coastal habitats and shallow off-shore banks (Durinck et al. 1994). Diet composition varies widely throughout their Holarctic range (Madsen 1954, Peterson and Ellarson 1977, Vermeer and Levings 1977, Goudie and Ankney 1986, Stempniewicz 1995, Bustnes and Systad 2001, Jamieson et al. 2001). However, few attempts have been made to relate feeding habits of Long-tailed Ducks to attributes of their local environment (Nilsson 1972, Stott and Olson 1973, Kube 1996). Long-tailed Ducks are recognized as opportunistic feeders (Peterson and Ellarson 1977, Goudie and Ankney 1986, Bustnes and Systad 2001), but ecological factors related to use of different habitats have received little study. We investigated food choice of Long-tailed Ducks wintering in two distinct marine habitats in nearshore waters of the Baltic Sea off the coast of Lithuania. Our objectives were to determine whether there were differences in diet choice of Long-tailed Ducks in the two winter habitats, and whether body condition of the ducks varied between the habitat types.

METHODS

Study area.—The Lithuanian coast can be characterized as an exposed, sandy coast, typical of the southern and eastern Baltic Sea (Oleninas et al. 1996). The sea floor is dominated by sand, gravel, or boulders. Sandy-bottom substrates predominated in the southern half of our study area along the Curonian Spit coast. The northern half of the Lithuanian nearshore zone is characterized by a mosaic of sediments of sand, gravel, and boulders (Oleninas et al. 1996). The sublittoral slope is gentle, with the 10-m isobath extending 700–2,000 m and the 20-m isobath extending 1,500–4,000 m from the shore. Water salinity along the Lithuanian coast is low, ranging from 6 to 8‰, which results in relatively poor faunal and floral diversity, as well as in low productivity.

Two main types of macrofaunal communities can be distinguished in the Lithuanian coastal zone: the *Mytilus edulis* community of sessile, epifaunal filter-feeders, and the *Macoma baltica* community of mobile, infaunal surface-deposit feeders (Olenin 1996, Oleninas et al. 1996). The *M. edulis* community dominates in the northern half of the Lithuanian coastal zone, occurring on hard bottoms covered by stones and boulders at depths between 5 and 30 m. This community has the highest biodiversity (up to 50 macrozoobenthos species) and biomass (mean = ~1,750 g/m², maximum = ~2,500 g/m² wet weight). *M. edulis* makes up ~93% of the total biomass; *Balanus improvisus* (a barnacle) and all the

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remaining species contribute ~7 and <1% of total wet weight, respectively. In some places, stony substrates at depths from 4 to 14 m are overgrown by the red algae, *Furcellaria lumbricalis*, which serves as an important spawning ground for Baltic herring (*Clupea harengus membras*; Olenin 1996, Oleninas et al. 1996).

The *M. baltica* community is associated with soft bottoms, and extends along the coast of the Curonian Spit at depths from 5 to 30 m. This habitat can be characterized as a homogenous, benthic biotope with up to 40 macrozoobenthos species dwelling in a sandy bottom. *M. baltica* and *Mya arenaria* are the dominant infaunal bivalves, composing 61 and 12% of the total biomass, respectively. Polychaetes (*Nereis diversicolor*, *Pygospio elegans*) and crustaceans (*Saduria entomon* and *Corophium* spp.) also are abundant. Mean zoobenthos biomass is ~150 g/m² wet weight, with a maximum of ~300 g/m² (Olenin 1996, Oleninas et al. 1996).

Based on spatial distribution and dominance of benthic communities (Olenin 1996; S. Olenin unpubl. data), three zones have been distinguished along the Lithuanian coast: a hard-bottom benthic community zone, an intermediate zone, and a soft-bottom community zone (Fig. 1). We present data on Long-tailed Duck foraging in hard-bottom and soft-bottom benthic community zones, but not the intermediate zone.

Data collection and analysis.—Birds accidentally drowned in fishing nets were collected for diet analysis during winters of 1997/1998 through 2000/2001. Nets were set at depths ranging from 1.5 to 20 m. In total, 326 Long-tailed Ducks were collected: 181 from habitats with hard-bottom and 145 from areas with soft-bottom substrates. Sex-age cohorts of collected birds in hard- and soft-bottom habitats, respectively, were as follows: immature males 13 and 14%; adult males 55 and 58%; immature females 16 and 8%; and adult females 16 and 20%.

The majority of collected birds were frozen within hours of collection. Frozen birds were thawed in a laboratory, dissected, aged, and sexed using the methods of Jones et al. (1982). Body fat was assessed by examining the subcutaneous fat layer on the upper abdomen, lower abdomen, and lower intestines.

Ranked categories of fat indices ranging from 0 to 3 were used for each deposit (0 = no fat and 3 = abundant fat), with overall fat scores calculated as the sum of the three indices (Jones et al. 1982). If not examined immediately, gizzards and esophagi were removed and deep-frozen or preserved in 4% formaldehyde solution until contents could be analyzed. Contents of gizzards and esophagi were treated separately, with material sorted, identified to the lowest possible taxonomic level, measured, and weighed. Each prey species was weighed separately except for small crustaceans, where gammarids were pooled without identifying specimens to species. Barnacles and bryozoans (*Electra crustulenta*) attached to mollusk shells were not considered as separate prey items; only loose barnacles were included in the analyses. The digestion stage of gizzard contents was assessed according to the following scheme: (1) food items intact, visually unaffected by digestion; (2) food at initial stage of digestion, soft prey still easy identifiable, much identifiable tissue; (3) food items heavily affected by digestion with some remains of tissues; and (4) food items heavily affected by digestion, no identifiable tissues remaining.

Diet composition was assessed according to wet weight of prey, including mollusk shells, from esophagi and gizzards showing stages 1 and 2 of digestion. Prey items were weighed to 0.01 g after removing surplus water by placing food items on filter paper. Data were summarized as the mean percentage of wet weight of each prey taxa per individual (Krapu and Reinecke 1992). Frequency of occurrence was calculated as the percentage of birds containing a certain food item. Inorganic materials (sand, pebbles, and amber) were excluded from subsequent analyses of content.

Preference of food objects in the two habitats was measured by Ivlev's selectivity index (Manly et al. 1993), calculated using the formula:

$$E = \frac{r_i - p_i}{r_i + p_i},$$

where r_i is the proportion of an item in the diet, p_i is the proportion of an item in the environment, and E is the selectivity index. Positive values indicate that the item is sought out

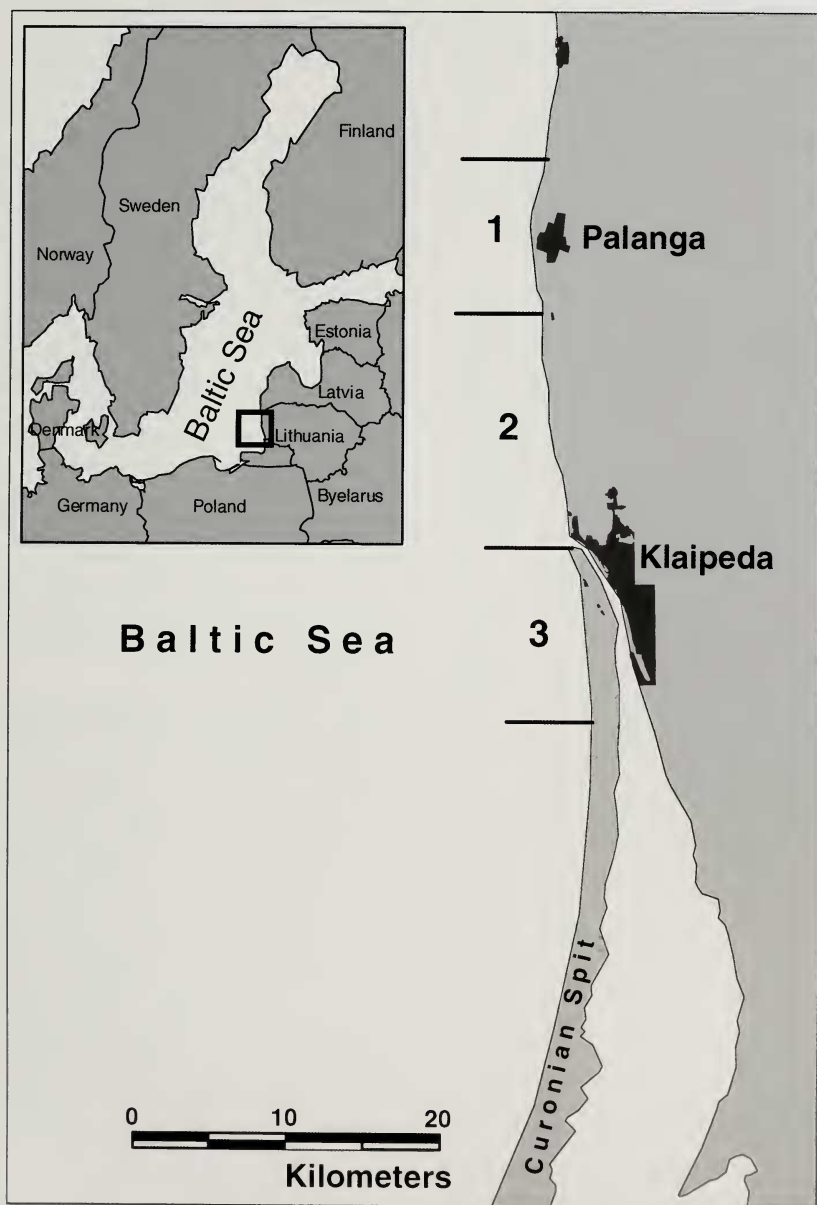


FIG. 1. Study area along the Lithuanian coast of the Baltic Sea and the three different habitat zones where the feeding ecology of Long-tailed Ducks was studied: (1) hard-bottom habitat, (2) intermediate zone, and (3) soft-bottom habitat.

in the environment and negative values indicate that it is not. To determine p_r , we used available benthos composition and biomass data that were collected in multiple sampling stations along the Lithuanian coast during 1980–1992. These data were summarized as average values (Olenin 1996, Oleninas et al. 1996), and correspond closely to those of oth-

er studies along the Lithuanian coast (Maksimovas et al. 1996, Bubinas and Vaitonis 2003). Because bivalve communities are considered to be relatively stable in the Baltic Sea (Kautsky 1982), we assumed that food resources utilized by Long-tailed Ducks during our study were well represented by previous studies (Olenin 1996, Oleninas et al. 1996).

We also assumed that the *M. edulis* community offers a rich and predictable food resource for Long-tailed Ducks, since the majority of *M. edulis* are of edible size, accessible to diving birds, and abundant (Daunys 1995). The *M. baltica* community was considered a poorer food resource due to low average biomass and because potential food objects are mostly buried in sand.

We conducted surveys to assess the abundance and distribution of wintering Long-tailed Ducks during four consecutive wintering seasons from 1997/1998 through 2000/2001. Survey areas were 10-km sections of shoreline along both hard- and soft-bottom community zones, with a 17-km gap between them (Fig. 1). Bird survey areas corresponded with the locations where ducks were obtained for diet analysis. We conducted bird counts from shore one to two times per month from December until April. Adverse conditions, such as choppy seas and ice floes, occasionally prevented us from conducting surveys. We used a spotting telescope (20–45×) and binoculars (10 × 50) to survey for birds on the water up to 2 km from shore. Bird abundance in the two habitats was summarized as mean number of ducks observed per linear km of shoreline surveyed. Statistical analyses were performed using Statistica 6.0 (StatSoft, Inc. 2001). We used nonparametric statistics to compare count and categorical data: a Kolmogorov-Smirnov test was applied to compare counts between two samples, Kruskal-Wallis ANOVA was used to compare multiple samples, and Mann-Whitney *U*-tests were used to compare data where sample sizes were low ($n < 20$; StatSoft, Inc. 2004). Standard deviations (SD) are given for means and statistical significance was set at $P < 0.05$. Considering the controversy surrounding the use of significance testing in the biological sciences (Cohen 1994, Johnson 1999), we also calculated effect sizes using the equation:

$$d = \frac{M_1 - M_2}{\sigma_{\text{pooled}}},$$

where d is the difference between means M_1 and M_2 divided by the pooled standard deviation, σ_{pooled} , which is defined as the square root of the mean of the two variances (Cohen 1988). Operational definitions for effect sizes

are small ($d = 0.2$), intermediate ($d = 0.5$), and large ($d = 0.8$; Cohen 1988).

RESULTS

Diet composition.—A total of 119 Long-tailed Ducks that fed over hard-bottom, and 87 that fed over soft-bottom substrates contained undigested food in gizzards and esophagi. At least 17 and 18 different prey taxa were ingested in hard- and soft-bottom habitats, respectively (Table 1). The actual number of prey species ingested was higher, as gammarids were pooled together without identification to species, and there were some specimens in other taxonomic groups not identified to species level. The few identified gammarids were *Gammarus oceanicus*, *G. salinus*, and *G. zaddachi*. The mean number of prey species ingested per Long-tailed Duck was 2.2 ± 1.1 ($n = 119$) in areas with hard-bottom and 1.9 ± 1.2 ($n = 87$) in soft-bottom habitat (Kolmogorov-Smirnov test: $Z = 1.33$, $P = 0.058$; $d = 0.28$).

Over hard-bottom substrates, *M. edulis* dominated in terms of wet weight and frequency of occurrence in the diet of Long-tailed Ducks (Table 1). The selectivity index for *M. edulis* was close to zero ($E = -0.05$, $p_{\text{edulis}} = 0.93$, $r_{\text{edulis}} = 0.85$), which indicates no active selection or avoidance. *S. entomon* was the dominant food type of birds that fed over soft-bottom substrates (Table 1). The selectivity index for this prey item was $E = 0.73$ ($p_{\text{entomon}} = 0.1$, $r_{\text{entomon}} = 0.63$), indicating that *S. entomon* was actively sought. Selectivity indices of bivalve clams in soft-bottom habitat were strongly negative for *M. baltica* ($E = -0.79$, $p_{\text{baltica}} = 0.61$, $r_{\text{baltica}} = 0.07$) and *M. arenaria* ($E = -0.54$, $p_{\text{arenaria}} = 0.12$, $r_{\text{arenaria}} = 0.04$).

Although *M. edulis* was the main prey species taken from hard-bottom habitat throughout the winter, Baltic herring spawn became the dominant food item in April, when it composed 68% of dietary wet weight (Fig. 2A). Crustaceans were the dominant food in soft-bottom habitat and did not fluctuate significantly between months (Kruskal-Wallis ANOVA: $\chi^2 = 3.08$, $df = 4$, $P = 0.54$; Fig. 2B; effect size d range: 0.05–0.50). We detected no significant sex- or age-related differences in diet composition in either habitat.

Fat score.—Mean fat scores of Long-tailed

TABLE 1. Diet composition of Long-tailed Ducks in soft- and hard-bottom habitats in the Lithuanian Baltic Sea, 1997–2001, expressed as frequency of occurrence (FO) and mean percent of wet weight (WW). Dominant food items are in boldface.

Prey	Soft-bottom (n = 87 birds)		Hard-bottom (n = 119 birds)	
	FO (%)	Mean % of WW (SD)	FO (%)	Mean % of WW (SD)
Algae	4 (4.6)	0.3 (1.7)	15 (12.6)	1.3 (9.4)
<i>Ceramium rubrum</i>			2 (1.7)	0.0 (0.0)
<i>Furcellaria lumbricalis</i>	1 (1.2)	0.1 (0.8)	13 (10.9)	1.1 (9.2)
Unidentified algae	3 (3.5)	0.2 (1.5)	4 (3.4)	0.3 (1.8)
Polychaetes	16 (18.4)	7.7 (24.4)	7 (5.9)	0.1 (0.3)
<i>Nereis diversicolor</i>	13 (14.9)	6.5 (22.2)		
Unidentified polychaete	3 (3.5)	1.2 (10.7)	7 (5.9)	0.1 (0.3)
Bivalves	32 (36.8)	14.5 (30.5)	113 (95.0)	86.8 (30.9)
<i>Cardium edule</i>	3 (3.5)	0.8 (5.7)		
<i>Macoma baltica</i>	14 (16.1)	7.2 (23.0)	5 (4.2)	0.4 (3.0)
<i>Mya arenaria</i>	15 (17.2)	3.6 (14.0)	10 (8.4)	1.0 (8.6)
<i>M. arenaria</i> siphons	1 (1.2)	0.8 (7.4)		
<i>Mytilus edulis</i>	4 (4.6)	2.3 (14.4)	110 (92.4)	84.6 (33.6)
Gastropods			11 (9.3)	0.1 (1.0)
<i>Hydrobia</i> sp.			8 (6.7)	0.0 (0.0)
<i>Theodoxus fluviatilis</i>			2 (1.7)	0.1 (1.0)
Unidentified gastropods			1 (0.8)	0.0 (0.1)
Crustaceans	71 (81.6)	74.3 (39.7)	27 (22.7)	3.7 (14.7)
<i>Balanus improvisus</i>	1 (1.2)	0.0 (0.0)	13 (10.9)	0.6 (2.2)
<i>Crangon crangon</i>	5 (5.8)	2.3 (14.2)	1 (0.8)	0.7 (8.0)
<i>Gammarus</i> spp.	4 (4.6)	0.0 (0.0)	11 (9.2)	0.6 (3.0)
<i>Idothea</i> sp.			1 (0.8)	0.0 (0.0)
<i>Mysis mixta</i>			1 (0.8)	0.0 (0.0)
<i>Neomysis integer</i>	10 (11.5)	9.1 (28.7)	2 (1.7)	1.3 (10.2)
<i>Saduria entomon</i>	62 (71.3)	63.1 (44.9)	2 (1.7)	1.4 (11.1)
Unidentified crustaceans	1 (1.2)	0.1 (0.6)	2 (1.7)	0.0 (0.1)
Fish	7 (8.1)	3.3 (12.9)	2 (1.7)	0.8 (6.7)
<i>Ammodytes</i> sp.	4 (4.6)	1.8 (9.6)		
<i>Clupea harengus</i> eggs			10 (8.4)	7.2 (24.7)
<i>Gasterosteus aculeatus</i>	1 (1.2)	0.1 (1.0)		
<i>Osmerus eperlanus</i>	1 (1.2)	0.5 (4.3)		
<i>Platichthys flesus</i>	2 (2.3)	0.1 (0.7)		
<i>Pomatoschistus</i> sp.			1 (0.8)	0.2 (2.7)
<i>Sprattus sprattus</i>	1 (1.2)	0.2 (1.8)		
Unidentified fish	2 (2.3)	0.7 (4.7)	1 (0.8)	0.6 (6.2)

Ducks collected from areas with hard- and soft-bottom sediments were 6.9 ± 1.9 ($n = 124$) and 7.4 ± 1.4 ($n = 93$) respectively (U -test = 5,061.0, $Z = -1.54$, $P = 0.12$; $d = 0.33$; Table 2). Over hard-bottom habitat, the mean fat score of adult males was significantly lower than that of immature males ($U = 317.5$, $Z = 2.86$, $P = 0.004$) and immature females ($U = 362$, $Z = -3.17$, $P = 0.002$). Over soft-bottom habitat, adult males also had the lowest fat reserves, which differed significantly from that of immature females ($U = 81.5$, $Z = -2.79$, $P = 0.005$); there were no

significant differences observed among other sex-age groups. Effect sizes among sex and age cohorts (Table 3) indicated somewhat similar relationships to those obtained by Mann-Whitney U -tests. No trend was observed in fat-score values over the course of the wintering season, and overall high fat-score values (>5) indicated that birds were in good body condition with considerable fat reserves.

Abundance and distribution.—Abundance of Long-tailed Ducks per linear km of shoreline over hard-bottom habitat (331 ± 544 , $n = 26$ surveys), was nearly 10 times higher

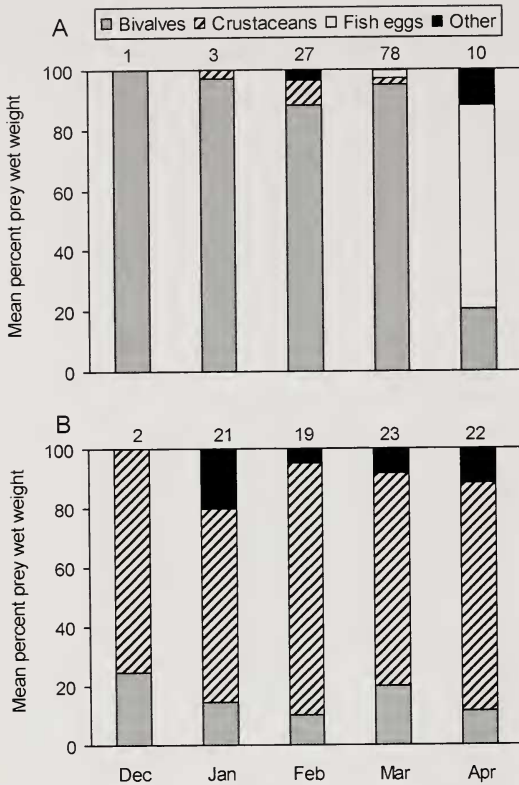


FIG. 2. Percent wet weight of prey taken by Long-tailed Ducks in the Lithuanian Baltic Sea, December–April, 1997–2001. Bivalves dominated the diet in hard-bottom habitat (A), with herring eggs being important in April. Crustaceans dominated the diet of birds in soft-bottom habitat (B). Sample sizes appear above bars.

than that over soft-bottom habitat (36 ± 23 , $n = 17$ surveys; $U = 60.5$, $Z = 3.99$, $P < 0.001$; $d = 0.77$).

DISCUSSION

Our results provide insight into the feeding ecology of Long-tailed Ducks in two contrasting coastal habitats of the eastern Baltic Sea. Marked differences were observed in Long-tailed Duck foraging patterns in different habitats. Differences involved numbers of birds using those areas, diet composition, and the degree of selectivity when choosing food items. However, body condition of birds was similar between habitats. The majority of Long-tailed Ducks occurred over rich, hard-bottom communities, where densities were approximately 10 times higher than in soft-bottom areas.

TABLE 2. Fat scores of Long-tailed Ducks in hard- and soft-bottom habitats along the Baltic Sea coast of Lithuania, 1997–2001. Birds were in generally good body condition (i.e., fat scores ≥ 5).

Habitat type/age class	Mean	SD	Range	n
Hard-bottom				
Immature males	7.7	2.0	3–9	17
Adult males	6.3	1.9	2–9	68
Immature females	7.8	1.7	4–9	20
Adult females	7.1	1.6	4–9	19
All birds	6.9	1.9	2–9	124
Soft-bottom				
Immature males	7.6	1.4	4–9	14
Adult males	7.1	1.4	4–9	53
Immature females	8.5	0.8	7–9	8
Adult females	7.8	1.3	5–9	18
All birds	7.4	1.4	4–9	93

Prey-item selectivity was very low in hard-bottom habitat, where birds fed primarily on the most available prey item, *M. edulis*. In April, ducks switched to feeding on fish eggs, when this temporary, but energy-rich, food source became available. Rich beds of *M. edulis* and spring herring spawn offer predictable food resources, so birds can ensure necessary energy intake with a given investment of effort. In contrast to hard-bottom habitat, Long-tailed Ducks exhibited a high degree of selectivity in soft-bottom habitat, where they foraged on the isopod, *S. entomon*, despite a benthic community dominated—in both biomass and abundance—by infaunal bivalves (Olenin 1996, Bubinas and Vaitonis 2003). In soft-bottom habitat, dominant bivalves were present at much lower densities, and some of them were unavailable because they burrow deeply into the sediment (Olenin 1996, Kube

TABLE 3. Effect sizes contrasting fat indices among age and sex cohorts of Long-tailed Ducks collected along the Baltic Sea coast of Lithuania, 1997–2001. Contrasts for hard-bottom sites are in the lower left portion of the table, with soft-bottom contrasts in upper right. See methods for interpretation of values.

	Immature males	Adult males	Immature females	Adult females
Immature males	—	0.41	0.76	0.10
Adult males	0.70	—	1.29	0.53
Immature females	0.05	0.82	—	0.69
Adult females	0.33	0.44	0.43	—

1996). Therefore, birds in soft-bottom habitat may not be able to rely on mollusks, and instead search for mobile, but more energy-rich, food items such as crustaceans. Although less available than sessile bivalves, species like *S. entomon* contain twice as much energy per unit wet weight as *M. edulis* (Rumohr et al. 1987); therefore, birds require less biomass to satisfy bioenergetic requirements.

Dominant prey of Long-tailed Ducks varies in different parts of the wintering range: gastropods are the predominant food item along the coasts of New Hampshire (Stott and Olson 1973) and northern Norway (Bustnes and Systad 2001); crustaceans are the most important prey for birds wintering at Lake Michigan (Peterson and Ellarson 1977), coastal British Columbia (Vermeer and Levings 1977), and Hudson Bay (Jamieson et al. 2001); and bivalves dominate their diet in the Baltic Sea (Madsen 1954, Nilsson 1972, Stempniewicz 1995, Kube 1996). Many authors agree that Long-tailed Ducks are opportunistic feeders, foraging on the most abundant and available prey (Peterson and Ellarson 1977, Goudie and Ankney 1986, Bustnes and Systad 2001). However, Jamieson et al. (2001) reported selective foraging by Long-tailed Ducks in polynyas (areas of open water in sea ice) of Hudson Bay, where birds fed almost exclusively on crustaceans, even though *M. edulis* were present. Jamieson et al. (2001) suggested that birds have to be selective by foraging on prey more profitable than *M. edulis* to meet energetic requirements in this harsh environment. Although bivalves generally dominate the diet of Long-tailed Ducks in the Baltic Sea, Stempniewicz (1995) found that males, which foraged at depths >20 m in the Gulf of Gdansk, fed exclusively on *S. entomon* isopods and suggested that only larger males are able to dive and feed efficiently at greater depths.

Assuming that animals attempt to maximize their net rate of energy intake by balancing food-item profitability and time spent feeding, the findings of our study can be discussed within the context optimal foraging theory (Pyke et al. 1977). If we assume that the rate of avian energy intake corresponds to the total biomass of macrozoobenthos, then Long-tailed Ducks would be expected to feed only in hard-bottom habitats where prey are abun-

dant and predictable. This theory is partly in agreement with our results, as we found a majority of Long-tailed Ducks occurring in rich, hard-bottom habitats. However some birds still used poor, soft-bottom areas and alternative explanations must be considered. Risk-sensitive foraging theory (Caraco 1980, 1981) may explain body condition of birds. This theory suggests that animals might make decisions to optimize a trade-off between food predictability in one habitat and greater maximum potential return in another (Caraco 1980, 1981). Guillemette et al. (1992) found that Common Eiders (*Somateria mollissima*) in good physiological condition in the Gulf of St. Lawrence used predictable habitats, where they foraged on blue mussels (*M. edulis*). Individuals in poorer condition, however, used a risk-prone foraging strategy and searched for more nutritious spider crabs (*Hyas araneus*) in habitat where prey abundance was low.

In our study area, Long-tailed Ducks used both productive hard-bottom habitat and areas with a relatively unproductive soft-bottom community. Risk-sensitive foraging theory (Caraco 1980, 1981) suggests that a nonselective foraging strategy among birds might be expected in rich, benthic communities, whereas an active searching strategy for particular food items might be employed in less productive habitats. Accordingly, Long-tailed Ducks foraging in rich, benthic communities should be in better physiological condition. Those in soft-bottom habitats should be in poorer or more variable condition. However, similar body conditions and variance estimates of Long-tailed Duck fat reserves in the two habitats indicate that Long-tailed Ducks—despite differences in productivity, foraging strategy, and food objects ingested—were able to attain similar (good) body condition. We speculate that the stable, and perhaps optimal, body reserves observed in Long-tailed Ducks throughout the wintering season indicate that birds are not energy stressed. Lower fat reserves in adult males may be due to higher energy expenditures during intensive courtship activities (RŽ pers. obs.) and/or better adaptability of males to the environment and a subsequent lower need to carry extra reserves.

The results of our study corroborate the

ecological plasticity of Long-tailed Ducks when selecting wintering habitats and choosing food items. We conclude that the majority of Long-tailed Ducks wintering in our study area actively select habitats and rely on the bivalve *M. edulis*. However, some of the population occurs in less productive habitats where they gain sufficient energy by foraging selectively on crustaceans.

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